Life History Traits of Two Allopatric Clupeids, Atlantic Menhaden and Gulf Menhaden, and the Effects of Harvesting on These Traits

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Abstract.—Life history traits of Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* were compared and interpreted within the context of a bet-hedging model that predicts what traits should evolve in local environments when the survival of the larval stage is less predictable than that of the adult stage. Atlantic menhaden appear to spawn in a relatively less-predictable environment. Compared with gulf menhaden, Atlantic menhaden are older at the onset of sexual maturity and have a longer reproductive span, as well as a longer spawning period. Atlantic menhaden produce larger eggs, and their larvae are larger at hatching and younger and larger at first feeding; the larvae appear to grow faster but they are relatively smaller than gulf menhaden at their first metamorphosis. Heavy exploitation of Atlantic menhaden has resulted in a truncation of the age structure, contraction of their spawning range, a reduction in lifetime fecundity, and possibly modifications of the egg size distribution. Thus, the risk of reproductive failure may have increased because spawning now takes place over narrower geographic and temporal ranges.

Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* are schooling, filter-feeding clupeids that are geographically separated but morphologically similar. They exhibit certain different adult life history characteristics (Nelson and Ahrenholz 1986; Ahrenholz et al. 1987) and early life history characteristics (Powell and Phonlor 1986; Powell 1993). They are a significant component of U.S. fishery landings. During 1990, Atlantic and gulf menhadens constituted 20% of the total fishery landings by weight (U.S. Department of Commerce 1990). The biological and environmental differences and similarities between these two species, coupled with an intensive fishery, suggests that a comparative study of their life histories can be important to fishery biologists and managers. Understanding how life history traits have evolved to allow populations to persist in their local environments, and how exploitation might alter these traits, is crucial to making proper management decisions.

The objectives of my study were to compare, from published data, the life histories of these two menhaden species within the context of life history theory (Stearns 1976) (1) to provide an insight into how these fishes have adapted to their local environments, and (2) to illustrate the value of life history theory in fisheries biology and management.

Life History Theory

Interest in the adaptive significance of life history reproductive strategies was stimulated by Cole (1954), who believed that species exhibit great variability in such characteristics as total fecundity, maximum age, and age-specific schedules of reproduction and mortality. Variability in these individual and population phenomena, Cole suggested, must favor population persistence in changing environments.

Cole's (1954) paper stimulated numerous life history studies, which have been aptly reviewed by Stearns (1976), who considered the key life history traits to be fecundity, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and the variation of these traits among an individual's progeny. Such traits are variable within populations, and, through natural selection, conspecific individuals belonging to different populations adapt to different circumstances.

The "life history theory" to which I refer in this article is that based on Cole (1954), Stearns (1976), and Endler (1986). In my use of the term "life history" here, I assume that traits of development, movement, and reproduction are (1) variable among individuals, (2) related to reproductive success and survivorship, or both, and (3) inheritable.

Two models resulted from life history theory—r- and K-selection, and bet-hedging—and these are employed to predict and explain traits in different environments. The r- and K-selection model predicts r-selection will operate when populations encounter variable and unpredictable environments on evolutionary time scales. Here, selection favors rapid growth and development, early age at sexual maturity, small body size, and semelparity (single spawning per lifetime followed by death). K-selection, on the other hand, will operate when populations encounter constant and predictable environments, which selectively favor slow development, delayed reproduction, larger body size, and iteroparity (multiple spawnings per lifetime) (Pianka 1970). This model should be visualized as an r–K continuum where no organism is completely r- or K-selected, but through trade-offs falls between the two extremes. An organism can be thought of as an r-strategist or K-strategist relative only to organisms in other populations of the same species or other similar species (Pianka 1970).

The bet-hedging model is an alternative model for the patterns explained by the r- and K-selection model (Sterns 1976). Using simulation models, Murphy (1968) advanced the argument that long life, late maturity, and many reproductive episodes are exhibited in environments in which density-independent factors cause wide variation in larval and juvenile survival, or in environments where intense competition exists between preproductives and reproductives. Murphy also argued that early reproduction, high fecundity, and few reproductions per lifetime can be exhibited in environments where adult mortality is high and variable.

Schaffer (1974) mathematically deduced a bet-hedging model in support of Murphy's (1968) arguments. Schaffer's model suggests that when environmentally induced variation in larval and juvenile survival occurs, the best adapted reproductive strategy would be reduction in reproductive output per spawning episode. Variation in adult survival, on the other hand, should result in greater investments in reproduction per spawning episode. Schaffer (1974) stated that this reasoning contradicts the generalizations that fluctuating environments favor greater reproductive efforts, whereas stable environments favor small litter size, slow growth, and increased longevity (i.e., r- and K-selection). The principal determining factor, Schaffer (1974) argued, is the age at which the organism is subject to the environmental fluctuation—that is, whether juveniles or adults are principally affected. The bet-hedging model, then, emphasizes the effects of environmental variability and unpredictability on juveniles. Most marine fishes have highly variable and unpredictable mortality during the larval–juvenile stage, and the bet-hedging model helps explain how life history strategies have evolved. The model predicts that among closely related species, those fishes in a variable and unpredictable reproductive environment will delay sexual maturity, have a longer reproductive lifespan, exert smaller reproductive effort per episode, and produce fewer, but larger, young per brood (Stearns 1976). I have used this model in interpreting the differences in life history traits between Atlantic and gulf menhadens.

Menhaden Life Histories

Atlantic menhaden range form Nova Scotia to Florida. From May to October, age-1 and older fish are distributed by age and size along the coast. The oldest fish live farthest north, and young-of-the-year fish occur in estuaries throughout the range. During the fall, fish north of Chesapeake Bay begin a southward movement, and by early winter fish of all ages are concentrated south of Cape Hatteras, North Carolina. During late winter and early spring, a northward movement occurs along the coast. Fish from Chesapeake Bay and northward continue to move north during the summer. Atlantic menhaden south of Cape Hatteras make little movement either north or south from June to November (June and Reintjes 1959; Roithmayr 1963; Nicholson 1971, 1978). This migration pattern results in a distribution of Atlantic menhaden of ages 3–11 in the northern part of their range (before intense fishing had an effect).

The spawning period of Atlantic menhaden is protracted, and it shifts seasonally. Nelson et al. (1977) gave a summary of the spawning cycle of this species that was based in large part on gonad maturation studies (Higham and Nicholson 1964) and systematic ichthyoplankton data from cruises (Reintjes 1961; Kendall and Reintjes 1975). Limited spawning occurs in spring off New Jersey and New York during the northward migration, as well as during the summer as far north as Cape Cod and occasionally in the Gulf of Maine. Spawning occurs well inshore and in bays and sounds from Long Island northward. During the early fall, spawning is widespread from southern New England to Virginia. Spawning intensity increases during the fall southward migration. By late fall and early winter, spawning is limited to areas be-

tween Delaware and North Carolina. Intensive spawning occurs offshore in the South Atlantic Bight during the winter, the only time during the year that adult Atlantic menhaden are not in coastal waters (Kendall and Reintjes 1975). Spawning may occur as far south as Florida but at a low intensity.

Gulf menhaden range along the Gulf of Mexico coast from Cape Sable, Florida, to Veracruz, Mexico (Reintjes 1969), but are harvested mostly off Louisiana and Mississippi (Nelson and Ahrenholz 1986), the likely center of distribution. Tagging (Kroger and Pristas 1975; Ahrenholz 1981) and exploratory fishing (Roithmayr and Waller 1963) revealed little to no movement of fish between areas east and west of the Mississippi River delta; as these fish increase in age, they gradually move toward the delta. Gulf menhaden overwinter on the inner and middle continental shelf just off the delta, and relatively close to the summer fishing area.

Gulf menhaden appear to spawn in depths of 2–110 m from Sabine Pass, Texas, to western Florida (Christmas and Waller 1975; Shaw et al. 1985). The center of spawning is from the Mississippi River delta west to the Atchafalaya River delta.

Gulf menhaden spawn mainly from September through April, with a peak in December (Christmas and Waller 1975; Shaw et al., 1985). Spawning begins in the north-central portion during October, and in November occurs throughout the north-central area and begins along the Texas coast. By December, spawning peaks along the north-central Gulf of Mexico and begins along western Florida. There is a slight decrease in January, but spawning is still intense in the northwest sector of the central Gulf of Mexico. A second peak of spawning in February was noted in the eastern sector of the central gulf. Spawning is less intense during March, and by April has mainly ceased. At this time, adult gulf menhaden return to nearshore waters and the commercial fishery commences.

Compared with gulf menhaden, Atlantic menhaden attain a larger maximum body size ($L\infty$), reach sexual maturity later, have a lower rate of natural mortality (M), and live longer (Table 1). The Atlantic menhaden reaches its maximum body size at a slower rate (k), but at any age, except age 1, it is larger than gulf menhaden. Age-1 fish of both species are similar in size. Growth of Atlantic menhaden is inversely related to stock size, whereas density-dependent growth of gulf menhaden has not been detected (Nelson and Ahrenholz 1986; Ahrenholz et al. 1987).

TABLE 1.—Summary of life history characteristics for Atlantic and gulf menhadens. Data are from Nelson and Ahrenholz (1986) and Ahrenholz et al. (1987).

Characteristic	Atlantic menhaden	Gulf menhaden
Maximum body size ($L\infty$)	363–373 mm[a]	253 mm
Growth rate (k)	0.3637–0.4539[a]	0.4748
Natural mortality rate (M)	0.45	1.1
Age at sexual maturity	2+ years	1+ year
Maximum age	10 years	4 years

[a] Range represents values from strong (1958) and weak (1967) year-classes. The first value is from the strong year-class.

There are considerable differences in early life history traits between laboratory-reared Atlantic and gulf menhadens (Table 2). Relative to gulf menhaden, Atlantic menhaden have larger and heavier eggs that contain a greater quantity of yolk (Table 2). Recently hatched larvae of Atlantic menhaden are relatively larger and heavier and contain a greater quantity of yolk reserves (Table 2). Development between hatching and first feeding is more rapid for Atlantic menhaden. This species has a higher rate of yolk utilization and more rapid development of structures associated with feeding (i.e., eyes, mouth, and gut) (Powell 1993), and it is younger at first feeding (Table 2). In addition, Atlantic menhaden are larger at time of first feeding and, at moderate to high temperatures (i.e., 20–24°C), grow faster and are much larger than gulf menhaden at 10 d past first feeding. Both menhadens undergo a body transformation during the larval phase (Powell 1993) and, after this transformation, there is a greater increase in body weight per unit length than before transformation. Transformation by Atlantic menhaden occurs at a smaller size (10 mm standard length, SL) than for gulf menhaden (12 mm SL). In summary, these menhadens appear to have two substantial differences in early life history traits. These are egg size and the influence of egg size on larval size, and the time spent in the early larval stage.

Late larval and juvenile life histories of these menhadens are difficult to compare, because of the lack of controlled experiments for these stages. Both species use estuaries during their first year of life. After entry into estuaries they undergo a complex series of metamorphoses from larvae to prejuveniles to juveniles. Concurrent with metamorphosis are internal changes related to feeding. They change from particulate feeders as larvae to filter feeders as juveniles (June and Carlson 1971). Most of the juveniles of both species leave estu-

TABLE 2.—Summary of data (mean values) for laboratory spawned and reared eggs and larvae of Atlantic and gulf menhadens. Values for specific temperatures are given only when temperature had a significant influence ($\alpha = 0.05$) on the trait. Data are modifications of those in Powell (1993).

Trait (at a certain temperature)	Atlantic menhaden	Gulf menhaden
Egg diameter (mm)	1.6	1.2
Egg dry weight (μg)	77.9	43.7
Egg yolk volume (mm^3)	0.583	0.483
Size at hatching (mm SL) at:		
16°C	3.4	3.1
20°C	3.2	2.6
24°C	3.2	2.8
Weight at hatching (μg)	49.8	39.3
Yolk weight at hatching (μg)	30.5	24.4
Yolk utilization rate ($\log_e$ mm$^3 \cdot$d^{-1}) at:		
16°C	−1.29	−1.17
20°C	−2.15	−1.74
24°C	−2.69 ·	−2.23
Age (d) at first feeding at:		
16°C	5.2	5.7
20°C	3.0	3.9
24°C	2.4	2.9
Length (mm SL) at first feeding	4.8	4.3
Growth rate ($\log_e$ mm$^3 \cdot$d^{-1}) at:[a]		
16°C	0.027	0.038
20°C	0.047	0.037
24°C	0.049	0.042
Length (mm SL) 10 d past first feeding at:[a]		
16°C	6.6	6.5
20°C	7.9	6.2
24°C	7.7	6.2
Size (mm SL) at first metamorphosis	10	12

[a] A species × temperature interaction was observed (Powell 1993).

aries during the fall and overwinter at sea (Reintjes 1969; Deegan 1986).

The Gulf of Mexico estuarine system supports a larger juvenile menhaden population (as estimated from age-1 fish) than the Atlantic estuaries, even though the two estuarine habitats have been estimated to be similar in size (approximately 1.1 million hectares) (Ahrenholz et al. 1989). The estimated biomass of the juvenile gulf menhaden population during the period 1964–1978 ranged from 182.0 × 10^6 kg to 616.1 × 10^6 kg (Nelson and Ahrenholz 1986). During the same period, the estimated biomass of the juvenile Atlantic menhaden population ranged from 37.3 × 10^6 kg to 398.7 × 10^6 kg (Ahrenholz et al. 1987).

Interpretation of Menhaden Life Histories

Menhaden Reproductive Environment

A comparison of the life histories of Atlantic and gulf menhadens, within the context of a bet-hedging model (Murphy 1968; Schaffer 1974; Stearns 1976), suggests that the Atlantic menhaden is adapted to a less predictable reproductive environment. But, as Leggett (1985) cautions, "correlation between measures of environmental variability and reproductive success," to assess life history theory models, "has too often been assumed rather than measured."

A major barrier to life history research is the difficulty in obtaining appropriate measurements of the environment (e.g., to determine whether it is stable or fluctuating, predictable or unpredictable) (Dobson and Murie 1987). Deciphering which environmental measurements appropriately relate to larval or juvenile survival of the menhadens is an impractical task because it requires long-term data series for multicausal factors. Indirect measurements of the environment that could provide insight into the predictability of the reproductive environment can be attained by examining processes in the spawning environment and population characteristics of the two menhadens. Large-scale processes that have an influence in the major spawning areas were examined.

The transport of Atlantic menhaden larvae from offshore waters to estuarine nursery areas has been reported as a major contributor to the relative success of an Atlantic menhaden year-class (Nelson et al. 1977). The transport process becomes increasingly important from the lower Middle Atlantic Bight to the South Atlantic Bight, because

Table 3.—The estimated fraction (S) of Atlantic and gulf menhadens surviving from egg to recruit, 1964–1976.

| Species | S | | High S : low S | Source |
	Mean ± SD	Range		
Gulf menhaden	0.00056 ± 0.00037	0.00021–0.00138	7:1	Nelson and Ahrenholz (1986)
Atlantic menhaden	0.00034 ± 0.00034	0.00007–0.00109	16:1	Ahrenholz et al. (1987)

spawning takes place progressively farther offshore as fish migrate southward in the fall. Nelson et al. (1977) showed that the greatest amount of variation in a recruit–environmental model could be accounted for by the strength of average monthly zonal (westward) Ekman transport south of Cape Hatteras, an area where substantial Atlantic menhaden spawning occurs. From this locus of intensive spawning, larvae must be transported up to 100 km to estuarine nursery areas. Checkley et al. (1988), on the other hand, hypothesized that the survival of Atlantic menhaden larvae spawned south of Cape Hatteras depended upon events other than Ekman transport, and on a scale of days (2–14 d) rather than months. When spawning coincided with the passage of winter storms, larvae drifted shoreward and food became abundant as a result of storm-induced upwelling and density-driven circulation. Regardless of the relative degree of importance of the two processes (Nelson et al. 1977; Checkley et al. 1988), stochastic events play a major role in the survival of Atlantic menhaden larvae.

The locus of intensive spawning for gulf menhaden occurs during winter in inshore waters between the deltas of the Mississippi and Atchafalaya rivers and relatively close to estuarine nursery areas (Shaw et al. 1985). Within this zone, peak spawning might occur at or in the vicinity of the Mississippi River plume (Sogard et al. 1987), which is a persistent oceanographic feature where high densities of gulf menhaden and macrozooplankton, and high levels of primary production have been reported (Govoni et al. 1989; Grimes and Finucane 1991). This system can, in turn, retain larvae, and a westward-veering frontal region interacting with a west–northwest longshore current could aid in the transport of larvae into estuarine nursery areas (Shaw et al. 1985; Govoni et al. 1989). A comparison of the two hypothesized loci of intensive spawning strongly suggests that the processes determining Atlantic menhaden larval survival are a result of relatively greater stochastic events, whereas processes determining gulf menhaden survival are a result of quasi-permanent currents and river flow.

The meridional distribution of Atlantic menhaden and the zonal distribution of gulf menhaden suggest that Atlantic menhaden face a relatively harsher reproductive environment because they range and spawn in both warm temperate and cold temperate zones, whereas the gulf menhaden spawns only in a warm temperate zone. Atlantic menhaden larvae have been reported to be absent from or reduced in numbers in estuaries during extreme cold periods; also, it has been hypothesized that severe winters, especially in the northern portion of the spawning range, result in heavy mortality of overwintering larvae–juveniles (see citations in Nelson et al. 1977). On the other hand, Nelson et al. (1977) argued that, because Atlantic menhaden spawn close to shore or in bays or sounds in the northern portion of their spawning range, they should be less dependent on currents for transport. By this reasoning, environmental factors influencing survival would be relatively stable, and variation in the number of spawners would be the probable cause of the variation in recruits produced.

Population characteristics of the two menhadens were compared to provide insight into the predictability and variability of their spawning environments. The estimated fraction of those surviving from egg to recruit during the period 1964–1976 was less for Atlantic menhaden than for gulf menhaden (Table 3). Estimates of the fraction of eggs surviving to recruit during this period varied 7-fold for gulf menhaden, whereas those for Atlantic menhaden varied 16-fold. Although variances around the mean estimated fraction were similar, the variability relative to the mean fraction surviving was greater for Atlantic menhaden than for gulf menhaden (Table 3). Stock–recruitment analyses of these two menhadens (Nelson and Ahrenholz 1986; Ahrenholz et al. 1987) suggest that there is only a marginal relationship between the number of Atlantic menhaden spawners and the number of recruits, indicating a strong density-independent influence. Gulf menhaden show a relatively better stock–recruitment relationship, in light of the inherent variability in clupeoid recruitment. That the relationship improves

TABLE 4.—The annual reproductive effort (grams dry egg weight per gram body weight) for Atlantic and gulf menhadens. Lengths for Atlantic menhaden were adjusted for density-dependent growth by averaging values from a strong (1958) and a weak (1967) year-class. Data were compiled from Lewis and Roithmayr (1981), Nelson and Ahrenholz (1986), Ahrenholz et al. (1987), Lewis et al. (1987), and Powell (1993). All values are means.

Age (years)	Fork length (mm)	Weight (g)	Fecundity (number of maturing ova)	Reproductive effort
Atlantic menhaden				
3	259	323	124,546	0.03
4	296	494	216,627	0.03
5	320	638	322,089	0.04
6	337	748	400,086	0.04
7	348	828	471,151	0.04
8	355	884	524,885	0.05
Gulf menhaden				
2	170	100	23,185	0.01
3	202	172	44,449	0.01
4	221	233	63,543	0.01

as spawning stock sizes increase indicates a probable strong density-dependent influence at moderate to high numbers of spawners.

The attempt to characterize the reproductive environment by examining population characteristics and hypothesized oceanographic processes, however, gives results that are only speculative. Therefore, the extent to which a bet-hedging model can be evaluated to link life history characteristics to the reproductive environment is limited. A major constraint is the lack of a recruit–environmental model for gulf menhaden similar to that developed for Atlantic menhaden (Nelson et al. 1977).

Early Life History Traits

The significance of egg and larval size has received considerable attention (see reviews or summaries by Mann and Mills 1979; Blaxter 1988; Miller et al. 1988; Hinckley 1990; Pepin 1991). Egg size is positively correlated with size at hatching, yolk reserves, size at first feeding, and mouth size. Larvae from larger eggs are less likely to starve, can swim faster and thus will prey more often, and probably can see better. Early survival should be higher for species that spawn large eggs (Miller et al. 1988), although Pepin (1991) questioned this conclusion. I concur with Pepin on the basis of findings (Powell 1993) that, although Atlantic menhaden larvae are larger and have higher growth rates than gulf menhaden at moderate to high temperatures, the gain in biomass (growth plus sur-

vival) by a cohort of early larvae over a range of prey concentrations did not differ between the two menhadens. These findings imply that relatively large Atlantic menhaden eggs that produced larger larvae were not at an advantage when prey concentrations were low.

The trade-off between larger sizes and greater numbers of eggs is a classical life history difference (Stearns 1980). On the basis of life history theory, gulf menhaden, which have relatively smaller eggs, would be expected to have a higher reproductive effort. But, if both of these menhadens are determinant spawners (i.e., the number of maturing ova indicate potential fecundity), gulf menhaden exhibit less reproductive effort than Atlantic menhaden (Table 4). Lower reproductive effort for gulf menhaden is contradictory to predictions of the bet-hedging model.

The adaptive significance of egg size is difficult to discern. In a bet-hedging model, selection favors larger eggs in uncertain reproductive environments. Pepin and Myers (1991) showed that neither egg size nor size at hatching influenced the cumulative stage-specific mortality rates of pelagic larvae. However, they found a significant correlation between change in length from hatching to metamorphosis and recruitment variability, implying that the longer the duration of the larval stage, the greater the number of factors that can influence survival and hence recruitment variability. Williams (1966) argued that accelerated development occurs in developmental stanzas in which mortality rates are high. Given that any life history characteristic that affects reproductive potential is subject to natural selection (Cole 1954), selection would favor a shortening of a stage that diminishes recruitment of the individual to the adult stock. Atlantic menhaden egg size might be, in part, responsible for not only size of larvae at first feeding, but more importantly, decreased age at first feeding (faster development) and time to first metamorphosis (Table 2). The concept that egg size is linked to stage duration is not novel. Kaplan and Cooper (1984) demonstrated that increasing egg size resulted in decreasing time to first feeding and decreasing time to metamorphosis in amphibians.

Adult Life History Traits

Increasing age at sexual maturity appears to be correlated with reduced adult mortality and subsequent increased fecundity in mammals (Harvey and Zammuto 1985). The greater age at sexual maturity in Atlantic menhaden could enhance re-

productive fitness if loss of fitness incurred by a lengthened juvenile period leads to gains related to some other trait (Williams 1966). Delayed maturity will be selected for if age-specific fecundity increases at a rate that will more than counterbalance a decrease in the rate of survivorship (Bell 1980). The high rate of adult mortality exhibited by gulf menhaden (Table 1) along with a relatively young age at sexual maturity are in accordance with Bell's (1980) argument. A relatively lower age at sexual maturity in gulf menhaden could be a result of the reproductive value of increased fecundity with age not counterbalancing higher adult mortality rates.

Atlantic and gulf menhadens exhibit markedly different reproductive life spans. This trait has received considerable attention from ecologists studying a wide array of organisms (see Stearns 1976 for review). Murphy (1968) argued that when there is uncertainty in larval and juvenile survival, there will be selection pressure for iteroparity. Roff (1981) reexamined Murphy's (1968) data and found that variation in reproductive life span was not an adaptation to variable reproductive success, but that reproductive life span is correlated with the age at maturity. Roff (1981) also showed that, for pleuronectids, variation in reproductive life span is a correlate of variation in age at sexual maturity, and brood success is linked to environmental conditions. Reproductive life span, then, is probably a response to unpredictable reproductive success. He argued further that the intrinsic rate of population growth, which depends upon age-specific survival and reproduction, will decrease with a delay in sexual maturity. For populations to persist with a delay in the age at sexual maturity, there must be an increase either in prereproductive survival, in reproductive output per spawning episode, or in reproductive life span. The link between age at sexual maturity and life span, and population persistence, as Roff (1981) argues, serves as a warning that the maintenance of the age structure may be crucial in managing species, like Atlantic menhaden, that have evolved a pattern of delayed maturity.

Compensatory responses (e.g., increase in fecundity, increase in growth rate, and decrease in age at sexual maturity) have been observed to occur with declines in fish stocks. Ware (1985) noted an increase in fecundity, increased size at age, and decreased age at first reproduction accompanying a decrease in biomass of Pacific herring *Clupea pallasi*. The net result was that size at first reproduction remained constant. Beacham (1983) noted a decline in median size and age at sexual maturity concurrent with a decline in biomass of Atlantic cod *Gadus morhua* in the northwest Atlantic Ocean. As growth rates of cod, like Atlantic menhaden, are inversely related to stock biomass, Beacham (1983) argued that faster growing fish attained sexual maturity earlier than slower growing fish. Jørgensen (1990) observed a decline in the age at sexual maturity for Atlantic cod in the northeast Atlantic region. Jørgensen suggested that the decline was a compensatory response to reduced stock size, but intensive fishing on relatively late maturing individuals that were geographically separated from early maturing individuals may also have contributed to the change. There is concern that compensatory responses to exploitation of Atlantic cod in the northeast Atlantic had adverse effects on the stock's reproductive fitness (Jørgensen 1990). Smaller fish are less fecund, and produce smaller eggs and larvae that might have a lower probability of survival than larger eggs and larvae. However, in this population of Atlantic cod the age structure, but not the size structure, has changed (Jørgensen 1990). Compensatory responses have not been detected in Atlantic menhaden populations. Lewis et al. (1987) looked at historical trends of Atlantic menhaden reproductive biology, but were unable to detect changes in fecundity over time. Their analysis was constrained by limited fecundity data for earlier periods and large interannual variation. Thus, their study does not negate the premise that changes in fecundity may have occurred.

Environmentally induced variation (i.e., phenotypic plasticity) is difficult to separate from genetically induced variation. These difficulties are especially inherent in intraspecific studies, and it has been suggested that different life history patterns exhibited by conspecific populations are probably the result of environmental influences (Dobson and Murie 1987; Jennings and Beverton 1991). Jennings and Beverton (1991) examined intraspecific life history differences in Atlantic herring *Clupea harengus* and argued that growth rate, maximum size, and longevity are temperature dependent and that life history traits, such as age at sexual maturity, should adjust to maintain evolutionary fitness. They observed that Atlantic herring stocks in waters of higher temperatures reach sexual maturity at a lower age and grow faster to maximum size than stocks in waters of lower temperatures. These differences are similar to those exhibited by gulf and Atlantic menhadens (Table 1). However, conclusions drawn from intraspecific
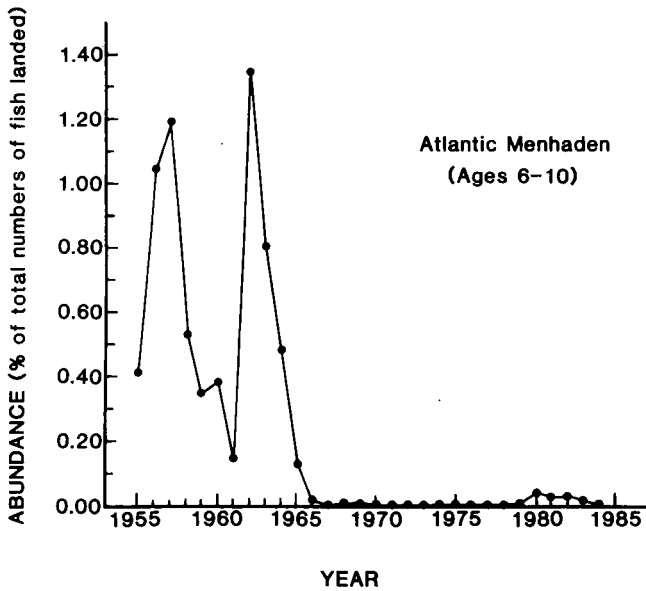
FIGURE 1.—Abundance of older Atlantic menhaden (ages 6–10), 1955–1985. Data are from Smith et al. (1987).

studies may not be appropriate to explain interspecific differences. For the latter, historical constraints on organismal design are most important (Dobson and Murie 1987). Hedges (1985) noted that interspecific differences in age at sexual maturity between similar-size tropical and temperate lizards could be explained by their geographic location rather than genetic variation. Species living in colder climates have a shorter growing season and therefore take longer to reach sexual maturity. Although gulf menhaden reach their maximum size at a faster rate than Atlantic menhaden, Atlantic menhaden are larger than gulf menhaden at any age except age 1, when they are similar in size. Although the growing season may be longer for gulf menhaden, Atlantic menhaden exhibit higher growth rates that result in larger size at age.

Effects of Harvesting on Life History Traits

Atlantic menhaden populations appear to have evolved age structures that offset the unpredictability of larval and juvenile survival. Historically, the population was composed of 10–11 age-groups, and such diversity allowed many repeated spawnings. But fishing has dramatically truncated the population age structure by virtually eliminating 6-year-old and older fish (Figure 1), and the population now consists of basically five age-classes (Smith et al. 1987). There appears to be a concomitant contraction of their spawning range because extensive migrations are age related. For

example, Ahrenholz et al. (1989) observed a decline in Atlantic menhaden juveniles, from 200 to 1 per trawl tow, during 1982–1986 in northern estuaries. The population has diminished ability for reproductive success because of fewer reproductive episodes in time and space. The truncation of the age structure has truncated the reproductive span and apparently reduced the net reproductive rate—the average number of age-0 offspring produced by each member of a cohort during its entire lifetime (Pianka 1983).

Older Atlantic menhaden (age ≥6 years) can make a substantial contribution to the population's egg production even though these age-groups represent a small proportion of the total population (Figures 1, 2). These age-groups can contribute greatly during the intensive winter spawning period when environmental conditions for transport are favorable. Nelson et al. (1977) showed that, when environmental factors (Ekman transport) are included in Ricker (1975) spawner–recruit calculations, the ascending slope is relatively steep for favorable environmental factors. Under these conditions, proportionately greater year-classes will be produced when spawning stock size is at an optimum. On the other hand, in years of poor environmental conditions in the South Atlantic Bight, recruitment would be low regardless of stock size (Nelson et al. 1977).

The contribution of older Atlantic menhaden can be substantial also in the upper Middle At-
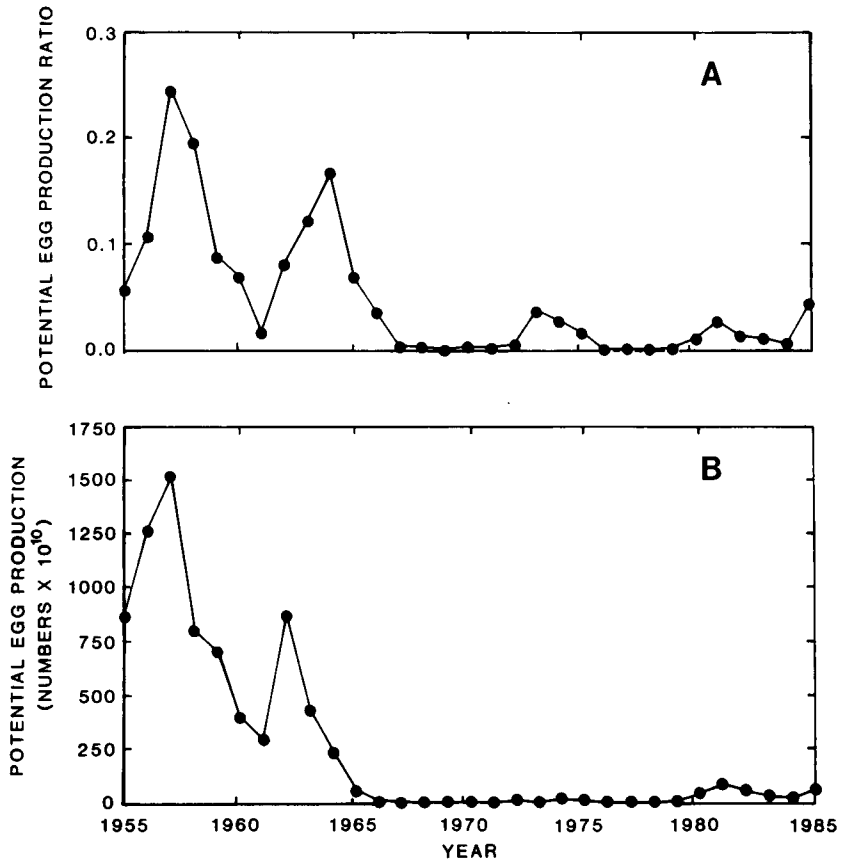
FIGURE 2.—Potential egg production for Atlantic menhaden. (A) Potential number of eggs that older fish (age ≥6) could have produced divided by the potential number of eggs that the total spawning population (age ≥3) could have produced, 1955–1985. (B) Total potential egg production for older fish (age ≥6), 1955–1985. Virtual population analysis data are from Vaughan (1993); fecundity data are from Lewis and Roithmayr (1981) and Lewis et al. (1987).

lantic Bight, where spawning takes place close to shore or in sounds (and ocean transport is thus reduced or eliminated). Here environmental factors influencing reproductive success are probably more stable, and stock size (i.e., number of eggs) is the probable cause of recruitment variability (Nelson et al. 1977). But the contribution of older Atlantic menhaden to the population's potential egg production, which averaged 11% during the period from 1958 through 1966, has for a long time been basically nothing (Figure 2). Moreover, a modification of egg size distribution toward smaller egg sizes within the population probably occurred, because egg size and age of spawning fish appear to be correlated (Powell 1993). Such a change could have a major impact on the early life history traits of Atlantic menhaden. Fishing pressure on Atlantic menhaden populations has altered their capacities to adapt to their environ-

ment, thereby affecting probabilities of long-term persistence of these populations. On the other hand, the exploitation of gulf menhaden populations has not altered the number of age-classes, and the population appears to be maintaining itself near historic levels (Nelson and Ahrenholz 1986). Over-exploiting gulf menhaden to the point of altering life history traits could have serious consequences, because the reproductive span of this species is relatively short.

Many have expressed concern over the alteration of life histories of various species through exploitation (e.g., clupeoids: Murphy 1967, 1977; Atlantic cod: Borisov 1978; American shad: Leggett and Carscadden 1978; long-lived groundfishes: Leaman and Beamish 1984). Recently, Sutherland (1990) questioned management strategies that recommend exploitation of larger fish and conservation of smaller fish as solutions for the

growth and recruitment problems caused by over-fishing. Sutherland argues that these size-selective policies could alter life histories and bring about long-term declines in yield. We need to recognize that the life history of a species is a direct reflection of the problems of survival and that altering life history almost certainly reduces the probability of long-term persistence of the populations and has potentially catastrophic consequences. Thus, we should approach fishery problems from a life history perspective as well as from a population dynamics perspective. As fishery biologists and managers, we should strive to maintain the diversity of life history and the evolutionary adaptive capabilities of fish populations.

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